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Three new species of *Vermipardus* Stuckenberg, and a revised cladogram for the genus with novel biogeographical implications (Diptera: Vermileonidae)

by

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ABSTRACT

Three new species of *Vermipardus* Stuckenberg 1960, are described: *V. barracloughi*, *trisignatus*, and *whiteheadi*. *V. barracloughi* is the first species to be found on the Drakensberg Escarpment in Mpumalanga Province; *trisignatus* and *whiteheadi* occur respectively in Afromontane forest and coastal scrubland in the South-West Cape. These three species clarify relationships and enable a new cladistic analysis of *Vermipardus* to be made. The previously defined *promontorii* species-group erected for two Cape Peninsula species is shown to be composite; *V. promontorii* (Stuckenberg) and *barracloughi* prove to be sister-species constituting a clade at subgeneric level, while *V. brincki* (Stuckenberg) is associated with *trisignatus* and *whiteheadi* in the newly-recognised *brincki* subgroup. Spermathecal structure in *Vermipardus* is described for the first time; two forms are found, corresponding to two basal clades. A revised cladogram is proposed, and sets of defining characters are given for all clades. The incidence of melanism in flies of this genus in the South-West Cape is discussed briefly.

INTRODUCTION

The genus *Vermipardus* Stuckenberg 1960, was redefined and revised in a previous study (Stuckenberg 1995). This is the most primitive afrotropical vermileonid genus. It is endemic to South Africa, occurring primarily in eastern and south-eastern montane regions of higher rainfall, on or seawards of the Great Escarpment (Fig. 1). It has not been found on the high plateau terrain of the eastern interior, or in the Karoo, in the relatively dry interior parts of the Eastern and Western Cape Provinces, or in Namaqualand. One species occurs in Lesotho and two on the Cape Peninsula. Most of the known species are in KwaZulu-Natal, but this may be a collecting artefact.

In my earlier study, *Vermipardus* was enlarged through the description of several new species, but it was conjectured that further species would probably be discovered, and that these might significantly change understanding of the genus. This has indeed happened. Thanks to the discovery by colleagues of wormlion populations in districts not previously searched, several interesting new species have been reared. In this paper three are described which are of special note, as they not only improve biogeographical knowledge of the genus, but also provide unexpected new insights into its cladogenesis.

In particular, it is now evident that the *promontorii* species-group, erected for the two species on the Cape Peninsula, is in fact not monophyletic. Two new species from the south-western part of the Western Cape Province (hereafter 'South-West Cape') show that a melanistic condition, on which the *promontorii* group had largely been based, is not a reliable indicator of relationships, but is a convergent feature of

Vermipardus species in that region. These two new species also diminish a large gap in the previously recorded distribution of *Vermipardus*, between the Cape Peninsula in the far west and the westernmost locality known for *V. londti* Stuckenberg, at Groot Rivier in the Knysna District.

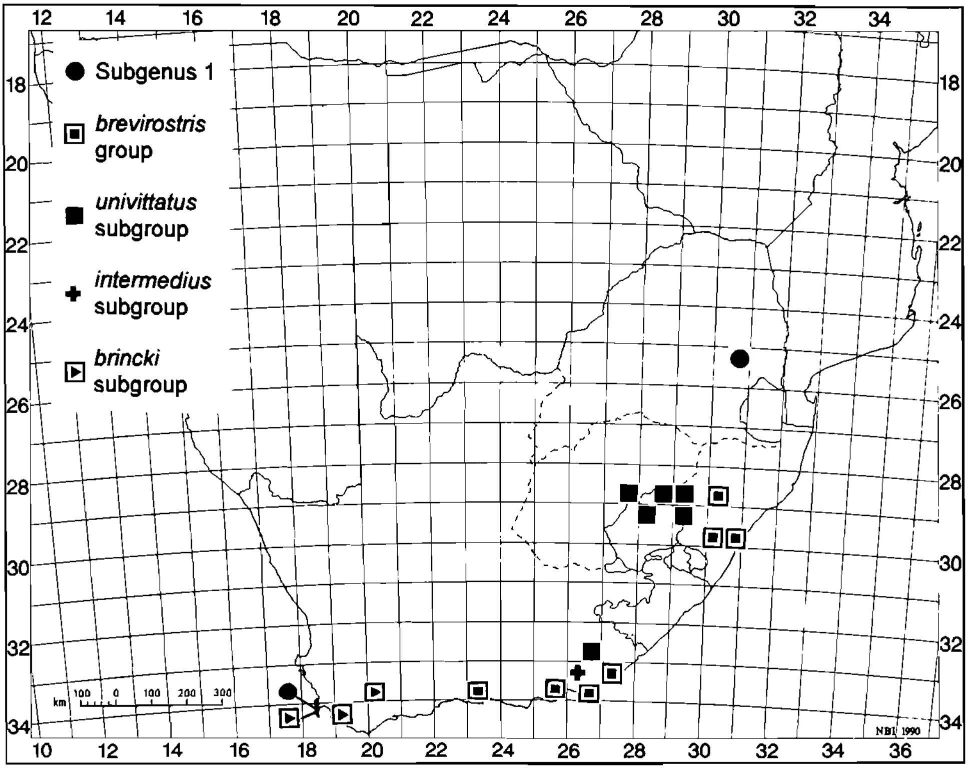


Fig. 1. Distribution of *Vermipardus* in South Africa. Subgenus 2 comprises the *brevirostris* and *univittatus* species-groups; the *univittatus* group is represented on this map by its three subgroups (see text). Both Subgenus 1 and the *brincki* subgroup of Subgenus 2 have a species restricted to the Cape Peninsula.

It had long been suspected that *Vermipardus* would be found to occur in the northern section of the Great Escarpment in the Mpumalanga and Northern Provinces (previously the Eastern Transvaal), as this would accord with the distribution of various palaeoendemic insect taxa which range along the entire length of the Drakensberg. The discovery of a wormlion population in the Sabie District by Dr David Barraclough has revealed the presence of a remarkable species, which most unexpectedly proves to be related to the distinctive species *V. promontorii* (Stuckenberg) of the Cape Peninsula.

Taking these discoveries into account, with a reassessment of the *promontorii* group, a new analysis of relationships within *Vermipardus* can be made. Although the genus is relatively small (13 species), it presents confusing and subtle systematic complexities which are only now coming to be understood.

MATERIAL AND METHODS

The specimens are pinned flies, mostly in the Natal Museum, Pietermaritzburg (NMSA), or in the South African Museum, Cape Town (SAMC), and the Albany Museum, Grahamstown (AMGS). Standard morphological terminology is used except as noted below. The preparation of genitalia, microscopical techniques, citation of label data, and terminology adopted for descriptions of male genitalia, follow previous practice (Stuckenberg 1995 1996). *Spiculae* are minute chitinous points on the outer surface of the aedeagus, appearing microscopically as flat, triangular projections. The *synsternite* comprises the fused hypandrium and gonocoxites; a ventromedian opening at its distal end is called the *ventral aperture*; *apical guides* are paired ventromedian extensions of the synsternite that narrow the distal end of the ventral aperture. 'Delta marks' are a pair of dark, sometimes fugitive, posteriorly-tapering markings anteriorly on the mesonotum, one on each side of the anterior end of the dark median vitta seen in most species (see the terminology of mesonotal markings in Stuckenberg 1995, Fig. 4). T = tergite.

The *proboscis ratio* expresses the relative size of the proboscis by dividing its length by the length of the fore femur as measured along its dorsal surface. The *radial fork ratio* was not used previously; it is calculated by dividing the length of R_5 (measured as a straight line, ignoring curvature of the vein) by the length of R_{4+5} (measured as a straight line from the furcation to the point of intersection with the r-m crossvein). This ratio may vary intraspecifically quite considerably, and even be different on the two wings of a fly; it is nevertheless useful for distinguishing unusual conditions of the radial fork. Available data show that most species have this ratio in the range of 0.58–0.68; in *V. promontorii* and *V. barracloughi* sp. n. the radial fork is much deeper, with a range of 0.75–1.0.

The material of new species was reared at my property in Merrivale, KwaZulu-Natal. Each larva was domiciled in a small glass jar (height 9.0 cm, diameter 6.5 cm) about half-filled with fine river-sand. The jars were kept on shelves in an outbuilding in which environmental conditions track those outside, but are moderated through the building being kept closed up. The larvae were fed mostly with male houseflies, at least twice a week to promote rapid growth.

A NEW SPECIES FROM THE NORTHERN DRAKENSBERG ESCARPMENT

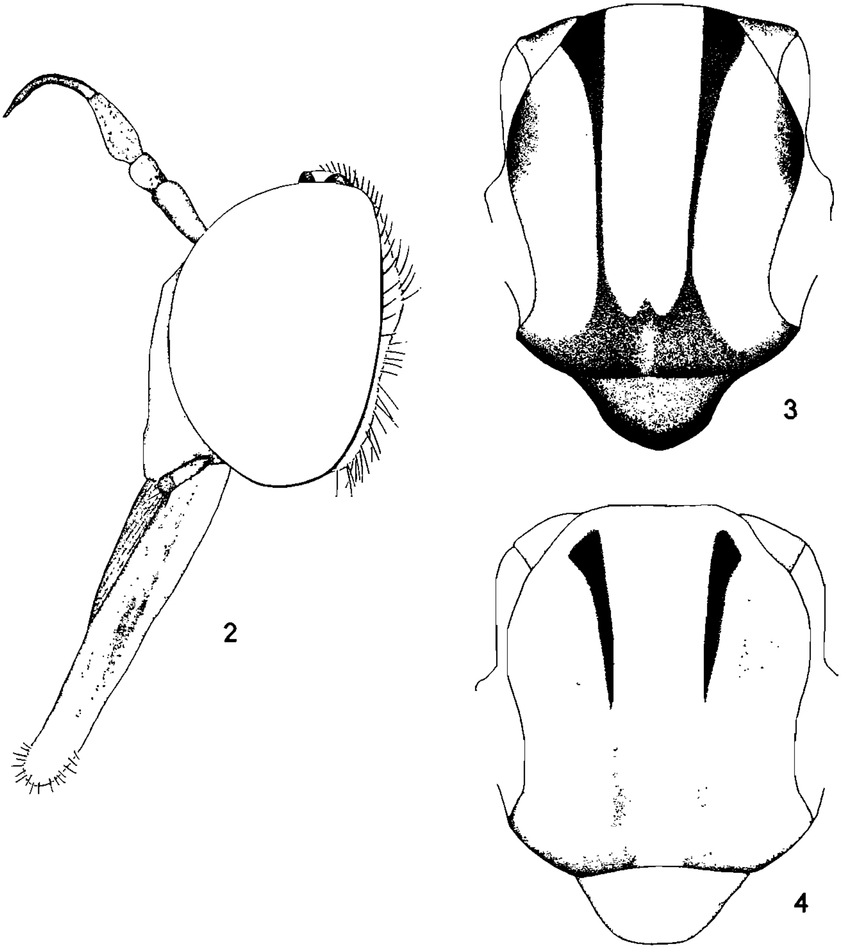
Vermipardus barracloughi sp. n.

Figs 2–6, 8–12

Etymology: Named in honour of Dr David Barraclough who discovered this interesting species.

Material examined: Holotype ♂ – SOUTH AFRICA: Transvaal #56/ Bridal Veil Falls/ 25°05'S:30°43'E 1500m/ Date: 3.iii.1995/ coll. D.A. Barraclough. Paratypes 3♂♂, 3♀♀, same data. Collected as larvae, reared by B.R.S.; emergence dates – ♂ 2.8.95, ♂ 20.8.95, ♂ holotype 4.9.96, ♂ 6.9.96; ♀ 21.8.95, ♀ 22.8.95, ♀ 25.8.95. Natal Museum Type No. 2197.

Diagnosis: Wing venation unique in lack of m-crossvein; mesonotal pattern scanty, comprising mostly only 2 weak delta-marks; proboscis shorter than fore-femur;



Figs 2–4. *Vermipardus barracloughi* sp. n. 2. ♂ head in lateral view. 3. ♂ mesonotum. 4. ♀ mesonotum.

conspicuous sexual differences in colouring, male having brown abdomen and dark hind legs with conspicuous whitish basal bands on tibia and basitarsus, female almost entirely dull orange, hind leg lacking contrasting pale bands; radial fork deep and almost symmetrical; R_{2+3} only moderately curved forwards apically; many unique hypopygial features (see below, and Figs 8–11).

Holotype ♂

Head (Fig. 2): Frons thickly dull greyish-brown pruinose, in some positions with fugitive sepia tinting; frons width at midlength equal to length, sides narrowly depressed along eye margins, medial area raised longitudinally and widening moderately towards ocellus; ocellar tubercle contrasting dark brownish-black; occiput shining pale silvery ashy-grey pruinose, with fugitive pale golden and sepia tinting emerging with changing angles of view; a narrow, dark brown median line from tubercle to cervix, and fugitive, dark velvety brown, subtriangular marks on upper occiput against eye margins. Antennae bicolorous, scape, pedicel and third segment yellowish-brown, remainder dark with minute, silvery-white microsetae; apical segment slender, elongate, apex pointed, about equal in length to segments 8+9. Face light brownish, thickly shining ashy-grey pruinose. Proboscis dark brown, distinctly shorter than fore femur, ratio for all males 0.7.

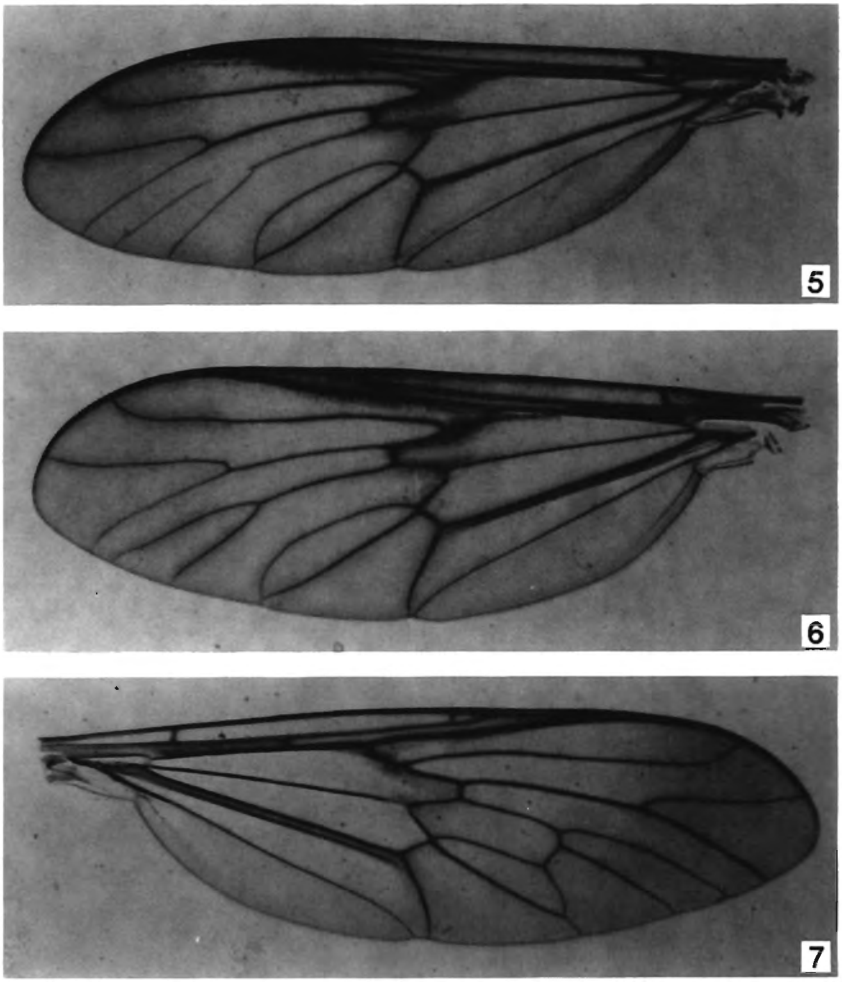
Thorax: Mesonotum (Fig. 3) reddish-brown, with limited pattern of strongly tapering, dark brown delta marks which become narrow and indistinct at mesonotal midlength, then reappear and expand posteriorly to unite medially in prescutellar area, where thin greyish pruinescence is present; narrow, pale midline stripe present, formed by moderately shining, dull yellowish pruinescence, similar pruinescence bordering outer edges of delta marks; downcurved sides of mesonotum darker. Halters blackish-brown. Scutellum weakly rugose transversely, both it and postnotum yellowish-brown. Pleura mostly pale amber-brown, with thin, weakly shining, greyish pruinescence; mesopleuron contrastingly apruinose, darker, glossy brown. Fore and middle femora uniformly light brownish; tibiae paler, almost whitish basally, with dense, shining, pale silvery-yellow microsetae; tarsi darker brown, grading apically to blackish-brown. Hind leg with femur uniformly darkish-brown above, indistinctly more reddish-brown ventrally; tibia conspicuously bicolorous, with a contrasting, short, whitish basal section which rapidly grades into blackish-brown for most of tibial length; hind tarsi also strongly bicolorous, most of basitarsus creamy-white, darkening apically, other tarsomeres blackish-brown; pale basal sections of tibia and basitarsus additionally conspicuous because of shining, pale golden, recumbent microsetae.

Abdomen: Markedly petiolate over segments 2–4, moderately broadening posteriorly; almost unicolorous, shining, medium brown dorsally. Hypopygium unusually short; resembling *promontorii* in lack of spiculae and presence of setose protuberances; otherwise so different that a comparison is required of Figs 811 with Figs 58 in Stuckenberg (1995); form of gonostyles compared in Figs 10 and 13; epandrium short, strongly arched transversely, without any form of concavity in posterior margin; distinctive in form of aedeagus, ventral aperture and apical guides.

Wing (Fig. 5): Membrane shining greyish-hyaline, without pattern except for weak clouding narrowly along R_4 and apical part of R_{2+3}, and brownish cloud in apical section of first basal cell; a moderately dark stigma in mature specimens; entire costal cell weakly smoky brown. Veins dark brown; median veins apically thin and weak; m-crossvein absent, discal cell thus open; cell m_3 either closed with very short stalk, or variably open; various abnormalities affecting M_{1+2} unequally featured on both wings of individual specimens – dichotomy of M_1 and M_2 may be absent, or M_2 complete while M_1 lacks basal section from point where dichotomy normally occurs, or M_1 and M_2 normal, but a short stump-vein off M_3 where m-crossvein would normally occur; R_{2+3} very moderately curved forwards over short apical section; radial fork almost symmetrical, R_4 weakly sinuous, fork unusually deep, ratio 0.73–0.92 for seven measureable wings, six of which have a range of 0.82–0.92.

Paratypes ♀ ♀

Head: As in ♂, except antenna less extensively darkened, scape yellowish-brown,



Figs 5–7. Wings of *Vermipardus* species. 5. *V. barracloughi* sp. n., ♂. 6. *V. barracloughi* sp. n., ♀. 7. *V. promontorii* (Stuckenberg), ♂ paratype.

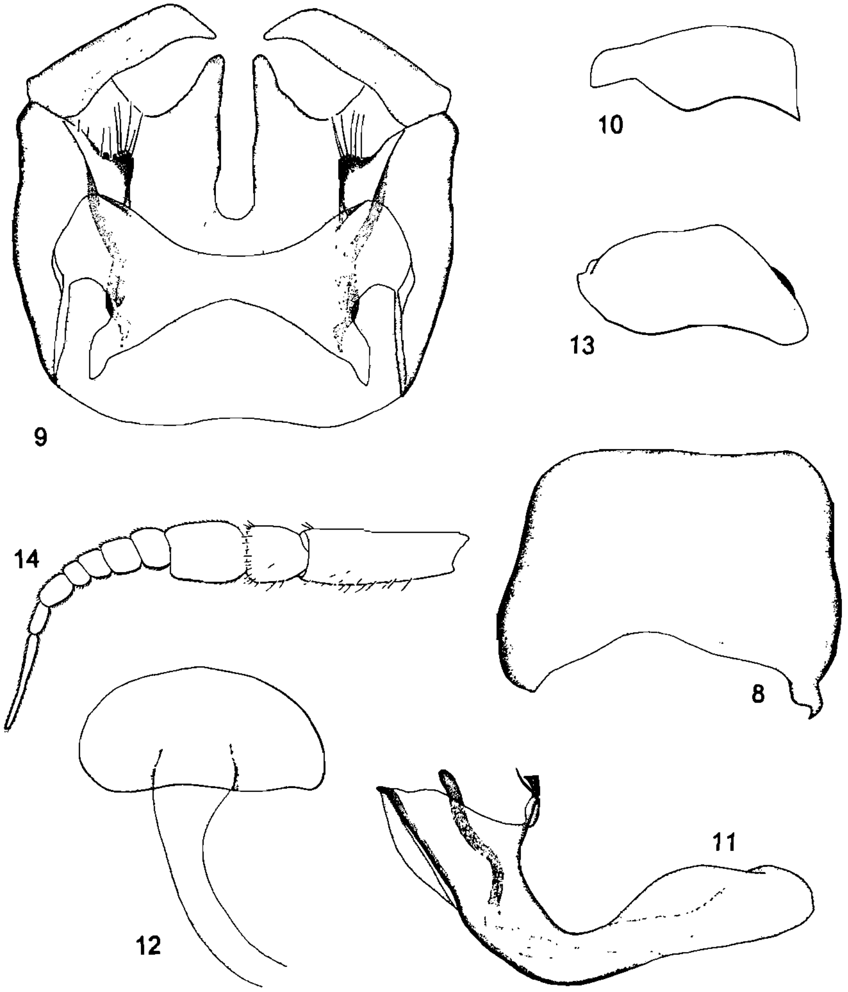
pedicel and segments 4–6 orange, 7–10 moderately dark brown. Proboscis ratio 0.67–0.73.

Thorax: Thorax and legs almost entirely yellowish-orange, mesonotum (Fig. 4) marked only by rather narrow, tapering, dark brownish delta marks, which almost disappear at level of transverse sutures then continue posteriorly into somewhat indefinite prescutellar marks which coalesce medially and are thinly silvery pruinose. Scutellum and postnotum yellowish-orange. Mesopleuron apruinose, shining, but not distinctly darker than other pleura. Fore and middle legs coloured like pleura, tarsi darkening apically. Hind femur brownish-orange, tibia paler basally but weakly so, grading into dull orange-brown; hind tarsus generally dark brown, basitarsus slightly paler basally.

Abdomen: Entirely orange-brown, a few internal, probably postmortem, dark marks. Spermatheca (Fig. 12) as described below.

Wing: (Fig. 6) Venational features as in ♂; all three ♀ ♀ have the fork of M_1 and M_2 fully formed; m-crossvein absent, in one specimen on both wings a short stump-vein where this crossvein would normally be; weak smoky brown staining in costal cell, otherwise only some weak brown stain around radial-sector and in stigmal area (all ♀ ♀ paratypes slightly teneral). Radial fork ratio ascertainable for two specimens: ♀ 1.09, 1.04; ♀ 0.93, 0.96.

Wing length: ♂♂ 8.2–8.9 mm, ♀ ♀ 9.1–10.4 mm.



Figs 8–14. *Vermipardus barracloughi* sp. n: 8. Epandrium in dorsal view. 9. Synsternite in dorsal view. 10. Gonostyle. 11. Aedeagus in lateral view. 12. Spermatheca. *Vermipardus promontorii* (Stuckenberg): 13. Gonostyle. *Vermipardus trisignatus* sp. n.: 14. ♀ antenna.

Notes: Flies of the two sexes of *barracloughi* are remarkably different in appearance. The generally darker male has a type of conspicuous hindleg patterning that occurs also in *promontorii* and the species of the *brevirostris* group (Stuckenberg 1995), whereas the almost uniformly dull orange female, with largely unicolorous hind leg, has a strong resemblance to the female of *V. univittatus* (Stuckenberg). The absence of the m-crossvein is unique as a specific character, although this condition occurs abnormally in one of the paratypes of *V. sylphe* Stuckenberg, from which a wing was removed fortuitously for a photograph (Stuckenberg 1995, Fig. 43).

Dr Barraclough informs me that he found the larvae in their pitfall traps at the base of a cliff bordering a path approaching the Bridal Veil Falls. The site was in deep shade, and had high humidity resulting from close proximity to the waterfall and to afromontane forest. Such a preference for shady, forested ravines is characteristic of several other species of *Vermipardus*. This is the only species that has been recorded to emerge in late winter (late August – early September), a trait possibly linked to the more northern latitude of the type locality.

TWO NEW SPECIES FROM THE SOUTH-WEST CAPE

Key to *Vermipardus* species in the South-West Cape

1 Wing (Fig. 7) with costal cell uncoloured, clear like basal cells, or at most with faint, smoky brown stain; R_{2+3} only moderately curved forwards apically; radial fork deep, ratio > 0.75; wing pattern weakly developed; hind basitarsus extensively whitish, contrasting conspicuously with dark brown tibia. [Cape Peninsula] .... **promontorii**

– Wing (Fig. 20) with costal cell strongly brownish, markedly darker than basal cells; R_{2+3} strongly curved forwards apically; radial fork shorter, ratio < 0.70 in nearly all available specimens; wing pattern strong; hind basitarsus inconspicuously whitish over very short basal section 2

2 Third antennal segment rounded and enlarged below, clearly deeper than succeeding segment (Fig. 27). [Onrus, Hermanus Dist.] .... **whiteheadi**

– Third antennal segment not distinctly curved below (Figs 14, 32), forming a smoothly tapering unit with succeeding segments 3

3 Smaller species (wing length ♂ 6.1 mm, ♀ 7.0 mm); ♂, epandrium with wide, shallowly curved posterior emargination; ♀, antenna bicolorous, scape and pedicel yellowish-brown, segments 3–10 dull blackish. [Cape Peninsula] .... **brincki**

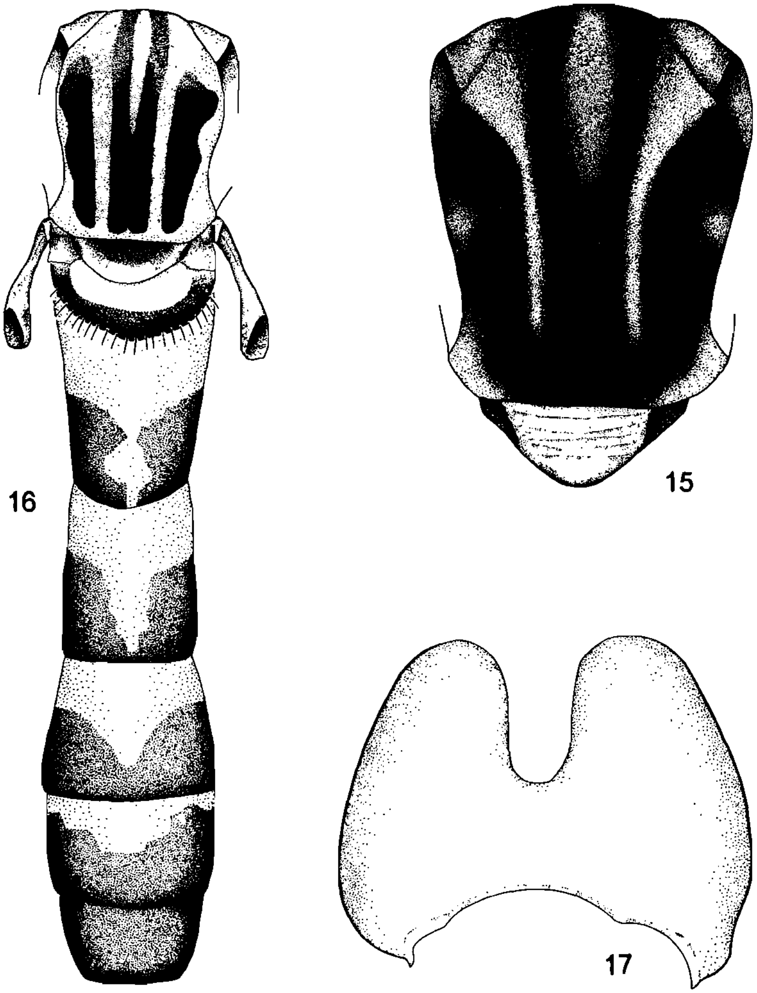
– Larger species (wing length ♂ 8.2 mm, ♀ 8.69.2 mm); ♂, epandrium deeply cleft by narrow, median emargination (Fig. 17); ♀, antenna blackish, scape and pedicel not contrastingly paler. [Langeberg Range, Swellendam Dist.] .... **trisignatus**

Vermipardus trisignatus sp. n.

Figs 14–20, 23

Etymology: *tri...* (L. three) + *signatus* (L. a mark), referring to the trivittate mesonotum.

Material examined: Holotype ♂ – SOUTH AFRICA: W. Cape #132/ Marloth Nature Reserve/ 33°59'S:20°27'E, 350m/ Date 26.ix.1995/ Coll: D. A. Barraclough/ Montane fynbos, forest. Paratypes – 3 ♀ ♀, same data. Collected as larvae, reared by B.R.S.; emergence dates – ♂ holotype 1.10.96, ♀ 2.10.96, ♀ 18.10.96, ♀ 24.10.96. Natal Museum Type No. 2198.



Figs 15–17. *Vermipardus trisignatus* sp. n. 15. ♂ Mesonotum. 16. ♀ mesonotum and abdomen. 17. Epandrium in dorsal view.

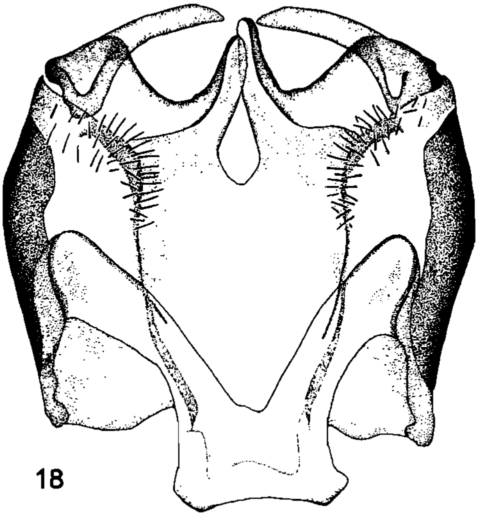
Diagnosis: Dark, glossy species with darkly patterned wing (Fig. 20); proboscis moderately short; hind legs much darker that other legs, only inconspicuously paler basally on tibia and basitarsus; R_{2+3} quite strongly curved forwards apically; marked sexual differences in mesonotal and abdominal patterning: ♂ mesonotum extensively shining blackish, with 2 narrow, curving lines of dull golden pruinescence demarcating a broad, median vitta, humeri amber-brown, scutellum entirely blackish, abdomen mostly blackish; ♀ mesonotum with 3 bold vittae surrounded by bright yellowish-orange, scutellum blackish on disc, yellowish-orange around margin, abdomen blackish with extensive pattern in orange or reddish-brown. Hypopygium unique in deeply cleft epandrium (Fig. 17) visible without dissection.

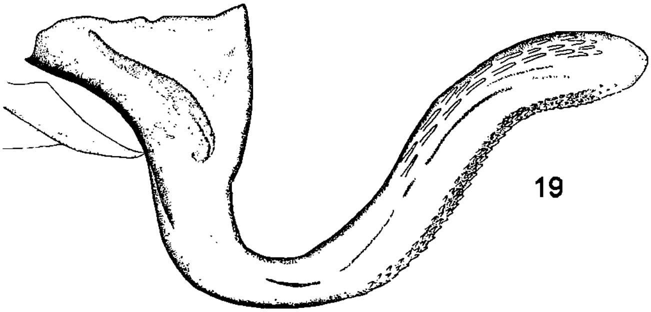
Holotype ♂

Head: Frons about as wide as long, narrowly depressed laterally along eye margins, median portion somewhat raised, thickly shining sepia-brown pruinose; ocellar tubercle shining blackish, a blackish medial occipital line from tubercle to a diffuse, fugitive, blackish-brown area above cervix; a narrow, intensely dark, velvety, elongate-triangular mark dorsally on occiput along each eye margin, occipital hairs dark. Face dark brown with sepia-brown pruinescence and small, fine, dark hairs. Antenna uniformly blackish, with minute silvery setae, relatively elongate, apical segment narrow and extended. Proboscis blackish, ratio 1.0, thus equal to length of fore femur.

Thorax: Mesonotum (Fig. 15) extensively shining blackish, with 2 curving, narrow strips of dull golden pruinescence which create a trivittate appearance, these strips terminating posteriorly at level of anterior end of postalar calli; humeral calli dull amber-brown; lateral declivous parts of mesonotum obscurely dark brownish posterior to transverse sutures. Scutellum entirely blackish, disc transversely rugose; postnotum shining blackish. Pleura extensively shining blackish-brown, upper part of hypopleuron dull yellowish-brown. Coxae shining blackish-brown like pleura, anterior pair less dark. Fore and middle legs almost uniformly yellowish-brown, tarsi darkened apically; hind legs mostly blackish-brown, femur less dark basally and also along ventral surface, narrowly yellowish-brown on extreme apex; hind tibia yellowish-brown over very short basal section (about ? of tibial length), basitarsus weakly pale basally.

Abdomen: Petiolate over segments 2–4; shining, mostly blackish except for dull orange-brown basal bands on T2–T5, bands of T3 and T4 more developed and occupying about $^1/_3$ tergal length. Epandrium deeply cleft in midline by elongate, almost parallel-sided emargination (Fig. 17). Hypopygium (Figs 17–19): epandrium large, lateral margins arching inwards, basal margin concave, distal margin deeply cleft by narrow, proximally curved, almost parallel-sided recess; synsternite deeply arched transversely, ventral aperture lanceolate, apical guides well developed as narrow, tapering, curved flanges approaching one another closely; gonostyles in dorsal view shallowly falcate, slightly incurved, tapering to obtusely-pointed apex; incurved dorsomedian surfaces with many conspicuous, thickened, stiff, erect, bluntly-terminated setae; dorsal bridge with elongate arms extending cephalad considerably so that bridge is positioned anteriorly to basal magin of synsternite. Aedeagus in lateral view with strongly upcurved shaft, its base expanding without deep incurvature on upper surface (contrast with *whiteheadi*, Fig. 30); spiculae numerous on shaft as illustrated.





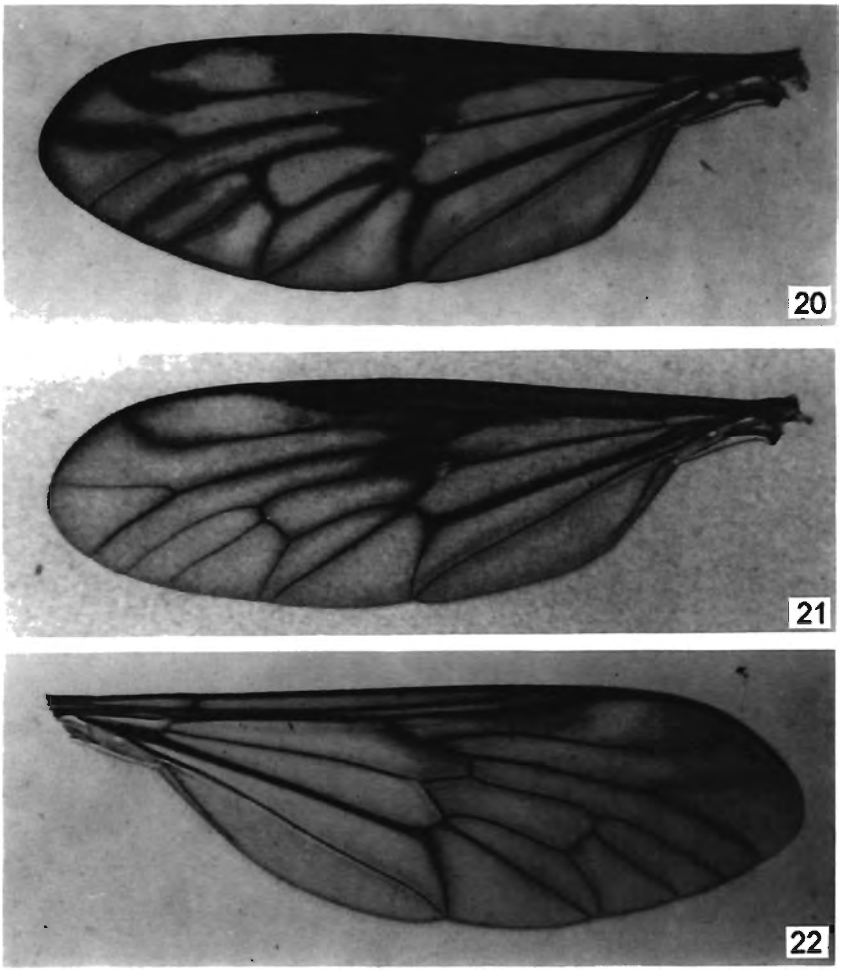
Figs 18–19. *Vermipardus trisignatus* sp. n. 18. Synsternite in dorsal view. 19. Aedeagus in lateral view.

Wing (Fig. 20): Generally dark smoky brown, with greyish areas within many cells; costal cell, stigmal area, apical part of first basal cell, and base of discal cell, dark brown; R_{2+3} strongly curved forwards apically; cell m_3 closed with a short stalk (an unreliable character, see ♀).

Paratypes ♀ ♀ . The three specimens differ in intensity and contrast of mesonotal and abdominal colouring, probably related to maturity at time of death. The following description is based on the specimen that emerged on 2.10.96, as it seems the most mature.

Head: Frons slightly wider than long, blackish in ground-colour, ashy-grey pruinose, lateral borders narrowly depressed along eye magins and apruinose; ocellar tubercle prominent, glossy black; occiput marked as in ♂; antenna blackish, except obscurely dark orange-brown basally on third segment; proboscis mostly blackish, ratio 1.2 (0.8 and 1.0 in other paratypes).

Thorax: Mesonotum (Fig. 16) glossy, bicolorous, boldly trivittate with black vittae; unlike ♂ in having vittae terminating posteriorly at a level a little posterior to anterior end of postalar callus; vittae separated by narrow, outwardly curving lines of greyish pruinescence; median vitta reaching anterior margin of mesonotum and enclosing an elongate fusiform, midline strip of rather weak, dull greyish pruinescence which terminates posteriorly at about level of transverse sutures; lateral vittae terminating midway between humeri and transverse sutures; humeral calli and surrounding area up to vittae, as well as declivous margins of mesonotum and a transverse prescutellar band, all bright yellowish-orange. Scutellum transversely rugose, basally blackish over much of disc, entire border yellowish-orange; postnotum shining dark brown over broad middle section, yellowish-orange laterally. Halter stem yellowish, knob fuscous. Pleura shining, blackish-brown over most of mesopleuron, lower half of sternopleuron, anterior half of pteropleuron, and lower third of hypopleuron, remainder yellowish amber-brown. Fore and middle coxae shining, warm yellowish-orange; hind coxae similar above, obscurely dark brown below. Leg colouration as in ♂; hind legs contrastingly darker than other legs, with short, pale basal section on tibia, a very short basal section of basitarsus weakly paler.



Figs 20–22. Wings of *Vermipardus* species. 20. *V. trisignatus* sp. n., ♀. 21. *V. whiteheadi* sp. n., ♀. 22. *V. brincki* (Stuckenberg), ♂ paratype, pattern faded in old balsam mount.

Abdomen: Boldly patterned dorsally (Fig. 16) in orange and black on T2–T5, T6 with narrow, poorly defined, transverse, basal band of brownish-orange; T1 entirely black, T7T9 appearing less shining because of abundant, short, recumbent, black setae. Spermatheca as described below.

Wing: Strongly patterned as in ♂, dark brown along veins, leaving greyish-hyaline areas within cells; stigma confluent with heavy brown marks in apex of first basal cell and base of discal cell; costal cell uniformly warm smoky brown.

Variation in other ♀ ♀ : Specimen that emerged on 24.10.96 has more darkly marked abdomen, pattern being reddish-brown and less contrasting; specimen of 18.10.96 has more extensive, somewhat darker orange markings on T5, and the same colour basally in an obscurely defined band on T6; venter mostly bright yellowish-orange.

Wing length: ♂ 8.0 mm, ♀ ♀ 8.6, 8.7 and 9.2 mm.

Notes: The larvae were found in their pits in soft earth sheltered by an overhanging rock. The site was in a thickly forested ravine, heavily shaded, humid, and close to a stream.

Vermipardus whiteheadi sp. n.

Figs 21, 27–31

Etymology: Named in honour of Dr Vincent Whitehead, who sent me larvae of this species from his property at Onrus.

Material examined: Holotype ♂ – SOUTH AFRICA/ W. Cape Prov.[-ince]/ Onrus [34°24'S, 19°11'E]/ Febr. 1996/ V. Whitehead. Paratypes – 2 ♀ ♀ , same data. Collected as larvae, reared by B.R.S.; emergence dates – ♂ holotype 19.9.96, ♀ 1.10.96, ♀ 20.9.96. Natal Museum Type No. 2199.

Diagnosis: Resembling *trisignatus* in general appearance, with similarly strong wing pattern; distinctive in ventral enlargement of third antennal segment in both sexes; proboscis a little shorter in both sexes than in *trisignatus*; ♂ has pruinose stripes of mesonotum shining greyish, and epandrium with a deep but much wider emargination than in *trisignatus*, also different form of aedeagus, lack of thickened setae on synsternite, and less extended dorsal bridge; ♀ has dark brownish scutellum (bordered with yellowish-orange in *trisignatus*), and generally darker abdomen, pale markings restricted to brownish-yellow patches laterally at base of T2–T4.

Holotype ♂

Head: Frons about as wide as long, pruinose ashy-grey with weak sepia tinting, sides depressed along eye margins, median portion biconcave; ocellar tubercle shining black; occiput pruinose like frons, pruinescence enclosing ocellar tubercle posteriorly, so no dark linear stripe present continuously from tubercle to cervix; blackish, velvety, subtriangular marks well developed along upper eye margins, and a roughly rounded, fugitive, dark brown mark on each side of upper occiput close to midline. Antennae (Fig. 27) elongate, distinctive because of ventral enlargement of segment 3 which is much deeper than segment 4; segments 4–10 comprise a compact, tapering series, individual segments not decreasing regularly in length, apical segment long, slender; scape and pedicel mostly dull yellowish-brown, darkened on dorsal surface; third segment yellowish-brown basally, blackish elsewhere and on segments 4–10. Face thinly ashy-grey pruinose, with faint sepia tinting; proboscis blackish, ratio 0.9.

Thorax: Boldly marked, extensively black with 2 strongly contrasting sublateral lines of greyish pruinescence; these demarcate a median vitta which is bordered anteriorly by short, velvety black delta marks; anteriorly this median vitta encloses a midline, elongate fusiform strip of brownish pruinescence; humeri and adjacent area below delta marks dull yellowish-brown, notopleural ridge posterior to humeri dark brown; dull brownish mark present in lateral part of transverse suture, extending along lateral mesonotal margin above wing; some thin greyish pruinescence on upper surface of postalar callus; scutellum flattened, transversely finely rugose, dark brownish-black except on sides which are basally brownish; thin greyish pruinescence on scutellar disc, margins shining apruinose. Postnotum shining dark brown. Pleura blackish on entire mesopleuron, most of pteropleuron, and lower parts of sternopleuron and hypopleuron; pleura generally with thin, shining, greyish pruinescence. Halter knob fuscous, base of stem dull yellowish-brown. Coxae of fore and middle legs dull yellowish-brown, hind coxae dark brown except on posterior surface which is dull yellowish-brown. Fore and middle legs pale amber-brown, darkened over apical tarsal segments. Hind legs with femur unicolorous brownish, darker on upper surface; tibia darker brown, dull whitish over very short basal section; basitarsus dull whitish basally, grading rapidly into brown, second tarsomere similarly brown, remaining tarsomeres darker brown.

Wing: Strongly patterned (Fig. 21), membrane greyish-hyaline, costal cell smoky brown, a dark brown stigma and similar mark around radial-sector; brownish infumescence narrowly borders most veins, leaving paler areas within cells; cell m_3 open in one wing, almost closed in other; R_{2+3} strongly curved forwards apically; fork of R_4 and R_5 quite deep (see below under *promontorii*), R_4 almost straight over much of its length between short basal bend and slight apical curve.

Abdomen: Slender and petiolate over segments 2–4; mostly shining blackish with weak, fugitive brownish tinge; T1 entirely dark; T2 narrowly dull orange-brown basally, this colouring expanded laterally; T3 and T4 very narrowly orange-brown basally; T5 with broader orange-brown basal band, about $^1/_3$ of tergal length; T6–8 lacking such bands basally, shining, with numerous semi-recumbent, dark hairs. Strongly contrasting, fugitive, silvery-grey pruinose bands present basally on T2–6. Epandrium transversely strongly arched, aedeagus protrudes prominently in dried holotype. Hypopygium (Figs 28–30): Epandrium large, margins incurved, basal margin concave , distal margin with large, deeply U-shaped recess; synsternite deeply arched transversely, ventral aperture narrowly lanceolate, apical guides formed as flanges curving posteriorly and approaching one another closely, incurved dorsomedian surfaces only with fine, sparse setae; gonostyles shallowly falcate, tapering to moderately acute point; dorsal bridge arms narrow, extended posteriorly so that dorsal bridge lies just cephalad of basal margin of synsternite; aedeagus in lateral view with almost straight shaft, apex slightly deflexed, with apicoventral recess, a strong incurvature (arrowed) in profile beneath flaring base; spiculae numerous on sides of shaft and on dorsal surface, as illustrated.

Paratypes ♀ ♀

Head: As in ♂; proboscis ratio 0.8 in both specimens; antennae and occiput as in ♂.

Thorax: Mesonotum (Fig. 31) generally as in ♂, the 2 sublateral, greyish, pruinose stripes enclose black delta marks anteriorly, and the median vitta similarly encloses an elongate fusiform, rather obscure, sepia pruinose, midline mark over anterior half. Scutellum dark brownish with thin greyish pruinescence on disc; postnotum shining dark brown, obscurely paler laterally. Legs as in ♂.

Wing: As in ♂; cell m_3 variably terminated, widely open to just closed at margin.

Abdomen: Shining blackish, with dark bluish tint on T1–3; T4–8 dark brownish-black; T2–4 with small lateral patches of brownish-yellow basally; shining bluish-grey pruinescence basally on T2–5, forming conspicuous bands when viewed obliquely from front.

Wing length: ♂ holotype 7.3 mm, ♀ 8.0 mm, ♀ 8.5 mm.

Notes: Dr Whitehead found the larvae on his property which is only about 50 m from the beach at Onrus. The larvae made their pits along walls of the house, but only where the ground was shaded and protected by nearby milkwood trees in the garden. The dominant natural vegetation in this now extensively built-up area used to be a coastal scrub composed mainly of milkwoods, with *Rhus* sp. and some fynbos elements.

NOTES ON THE CAPE PENINSULA SPECIES, AND THE FACTOR OF MELANISM

In my previous study (Stuckenberg 1995), an attempt was made to assess relationships between the ten species of *Vermipardus* known at that time, and three species-groups were recognised, viz. the *promontorii*, *brevirostris* and *univittatus* groups. The first-named contained two species known only from the Cape Peninsula, *V. promontorii* (Stuckenberg) and *V. brincki* (Stuckenberg). This group was defined mainly on the basis of exceptional melanistic colouring not occurring in any other species. Both peninsular species have a largely blackish mesonotum marked conspicuously by two slender, sublateral stripes of pale greyish or silvery pruinescence. The sympatry of these species on the Cape Peninsula, and their remoteness from the nearest *Vermipardus* species known then (in the Eastern Cape Province), supported the perception that they might be related. But doubts were expressed that this was a natural group: it was pointed out that *promontorii* has unique hypopygial features, such as a lack of aedeagal spiculae; and that *brincki* has features found in the *univittatus* group, viz. falcate gonostyles, a small, very narrow ventral aperture, and elongate, slender, closely approximated apical guides, as well as subdued patterning of the hind leg.

The discovery of the three new species described above provides new insights into relationships within *Vermipardus*. It is shown below that the *promontorii* group in fact is not monophyletic, and that the following situation exists:

- *barracloughi* of the northern Drakensberg Escarpment proves to be a sister-species of *promontorii*, the two forming a basal clade at subgeneric level;
- all other known species form a monophyletic clade of equivalent subgeneric rank;
- *brincki* and the other new species described above form a clade with the following structure: *brincki* + (*whiteheadi* + *trisignatus*).

The confusing factor among peninsular species was melanism, as it produced a strong similarity in general appearance and colouring, now seen to be convergence. It is noticeable that *whiteheadi* is also a dark species; perhaps not coincidentally, it occurs close to the Cape Peninsula and very near the sea. *V. trisignatus* is also generally dark, but it has a more richly contrasting colouring, especially in the female. Both *brincki* and *whiteheadi* live in relatively low shrubland, whereas *trisignatus* occurs in afromontane forest on the Langeberg Range, further east and much more inland, where the climate is not maritime.

Another case is on record featuring melanism. Usher (1972), in her survey of the South African horseflies (Tabanidae), outlined extraordinary variation she discovered in the widely-distributed species *Haematopota ocellata* Weidemann. This species was found to be relatively constant over much of its range in the Eastern and Western Cape Provinces and in KwaZulu-Natal. In the South-West Cape, however, specimens from close to the coast were distinctive, being much darker with heavily patterned wings, the darkest specimens coming from the southern end of the Cape Peninsula. Specimens from the interior showed increasing paleness correlated with declining rainfall and higher altitudes, and the phenomenon of xanthochroism appeared, with components of the patterning becoming yellow. Specimens with such coloration from the Nieuwoudtville area and Lesotho had been described as another species, *H. spectabilis* Oldroyd, but Usher considered this to be just an extreme variant.

The question arises as to whether the cool, damp climate associated with the cold sea around the South-West Cape could result in increased melanism in these flies at sites close to the coast, and particularly on the Cape Peninsula. It is well known and an often-stated general observation, that melanin production tends to occur in insects that pupate in cold, damp seasons or localities.

Vermipardus promontorii (Stuckenberg)

Figs 7, 13

Lampromyia (Vermipardus) promontorii Stuckenberg 1961: 120–124.
Vermipardus promontorii, Stuckenberg 1995: 226, Figs 5–8 (♂ genitalia).

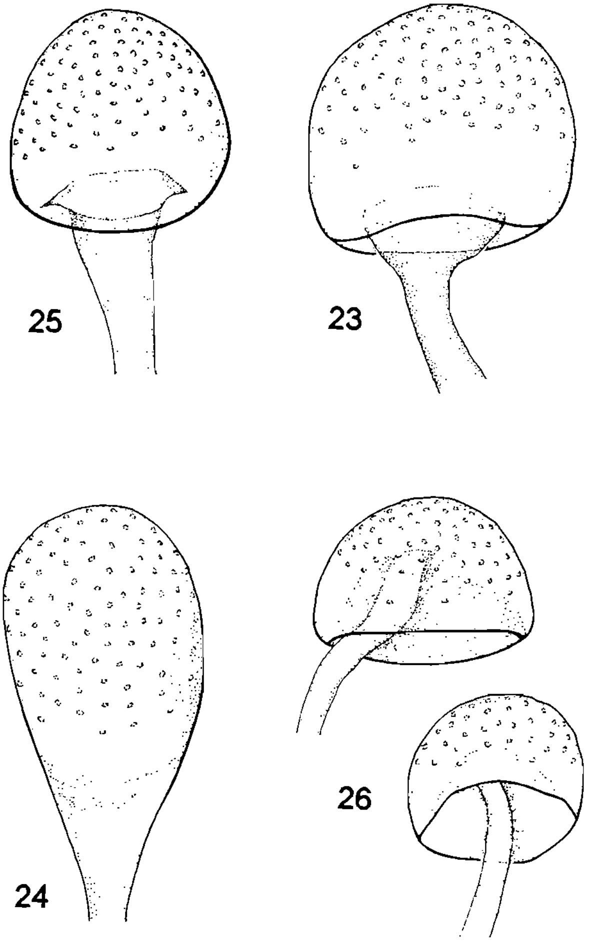
The following data are derived from further studies of the type series and other specimens recorded by Stuckenberg (1995).

Wing (Fig. 7): Pattern unique; a smoky infusion occupies entire apex inwards to fork of R_4 and R_5, extending obliquely to apex of cell m_3; a brownish stigma in apex of subcostal cell, a brownish cloud around radial-sector and in apex of first basal cell; otherwise wing is hyaline, with well-developed microtrichia on membrane. R_{2+3} gently sinuous, only gradually and moderately curving forwards apically; radial fork almost symmetrical, unusually deep as revealed by radial-fork ratio in following table:

promontorii	♂ 0.75–1.0; ♀ 0.96 (< 0.80 only in two wings)
brincki	♂ 0.66
whiteheadi	♂ 0.68–0.72; ♀ 0.48–0.70
trisignatus	♂ 0.51–0.56; ♀ 0.49–0.62

Cell m_3 closed and stalked in all specimens of type series; in ♂ from Table Mt slopes above Cape Town, closed at margin in one wing; in ♂ from Cape Point Nature Reserve, narrowly open in both wings.

Terminalia of ♀ : Unique in following features: T8 and T7 with small median notch in basal margin; T9 deeply incurved proximally, extensively sloping postero-dorsally as a prominent 'hood' over proctiger; cerci with basal segment asymmetrical, lower lobe more protruding and narrower than upper lobe, apical segment greatly reduced to an almost linear stub in apical recess of basal segment.



Figs 23–26. Spermathecae of *Vermipardus* species. 23. *V. trisignatus* sp. n. 24. *Vermipardus* sp. indet., Kloof, *brevirostris* group. 25. *V. univittatus* (Stuckenberg), Cathedral Peak. 26. *V. intermedius* (Stuckenberg), Grahamstown, two spermathecae in different positions.

Vermipardus brincki (Stuckenberg)

Figs 22, 32–33

Lampromyia (Vermipardus) brincki Stuckenberg 1960: 253257.
Vermipardus brincki, Stuckenberg 1995: 226.

The following data are derived from the ♂ paratype in NMSA.

Antenna: Available material incomplete, lacking apical segments, as in Fig. 32; original description stated 'Apical segment of antennal style like a short arista [ie. very slender], a little less than $^1/_3$ combined lengths of whole style and third segment.'

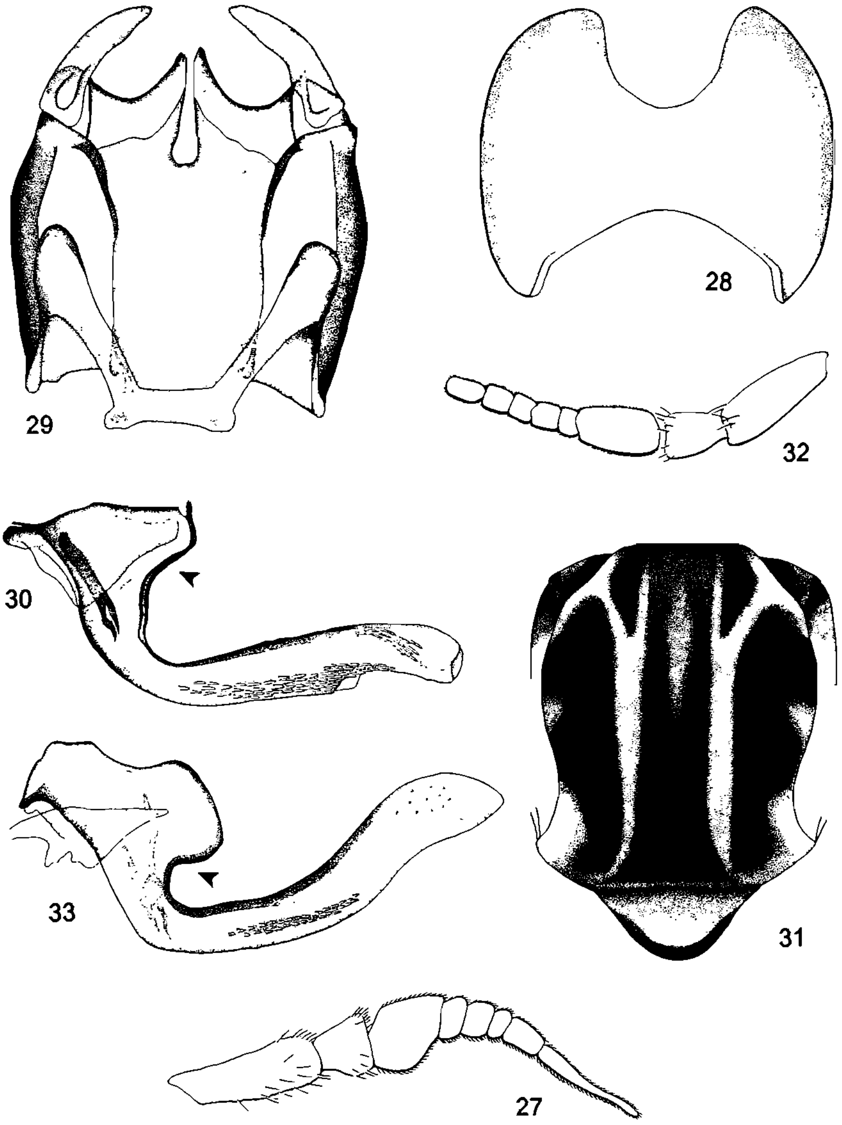
Thorax: Mesonotal pattern as in *whiteheadi*; extensively blackish, appearing trivittate because of 2 anteriorly curved sublateral stripes of greyish pruinescence; humeri dull orange-brown, this colour also forming small lateral mark in transverse suture; median vitta enclosing poorly-defined midline stripe of thin sepia pruinescence which tapers posteriorly; lateral vittae not reaching posterior edge of mesonotum where orange-brown of postalar calli is continuous; pleura coloured as in *whiteheadi*, postnotum shining warm brown. Legs as in *whiteheadi*; hind femur and tibia shining, moderately yellowish brown, both slightly darkened apically, extreme apex of femur dull yellowish; hind tibia weakly paler at extreme base only, hind basitarsus also only slightly paler at base.

Wing: Two wings in old balsam mounts now faded, original pattern still discernible (Fig. 22).

Abdomen: Strongly petiolate over segments 2–4; mostly blackish-brown, with very short, poorly defined, obscure brownish or yellowish-brown, transverse, basal bands on T2–T5, these bands more developed and yellower laterally. Hypopygium differing clearly from other subgroup species in shape of epandrium (much shorter, with broad, shallow recess in hind margin), and shape of aedeagus (Fig.33, shaft straight over middle section, moderately upcurved apically, base strongly incurved on posterior surface as in *whiteheadi)*, spiculae numerous on shaft.

SPERMATHECAL FORM IN VERMIPARDUS

During a revision of the palaearctic species of *Lampromyia* Macquart, it was found that spermathecal form could be used to characterise species-groups in that genus (Stuckenberg 1997). It seemed promising, therefore, to investigate these structures in *Vermipardus*; the results, as described below, proved to be important for the identification of principal lineages. Unfortunately, the widely differing spermathecal forms found in both genera pose problems in cladistic analysis, as the characters displayed can seldom be polarised with confidence. Outgroup comparison with other afrotropical vermileonid genera has not been helpful, and no transformation series is apparent. A preliminary survey of literature on the Brachycera suggests only that two assumptions may be valid in regard to the wide range of spermathecal forms found: 1) a simple condition (ie. without structural elaborations) is plesiomorphic; and, 2) the spherical condition may be plesiomorphic. If they are valid, the larger, mushroom-shaped form of *promontorii* and *barracloughi* would be a synapomorphy; the smaller, simpler form of all the other species appears to be less specialised, but its distinctive surface granularity is surely a synapomorphy.



Figs 27–33. *Vermipardus whiteheadi* sp. n.: 27. ♀ antenna. 28. Epandrium in dorsal view. 29. Synsternite in dorsal view. 30. Aedeagus in lateral view. 31. ♀ Mesonotum. *V. brincki* (Stuckenberg): 32. ♂ antenna, incomplete. 33. Aedeagus in lateral view, the deep incurvature found in this species and *whiteheadi* marked by arrows.

The scarcity of female specimens of several species has limited this investigation. All that could be done was to examine one species from each of the lineages. The extent of interspecific differences in spermathecal form within species-groups is thus unknown. The following results were obtained:

1. *V. promontorii*, paratype. Spermatheca pale, mushroom-shaped, with a broad,

shallow, smooth, moderately curved cap, and a simple, pale duct attached centrally below (see next species).

2. *V. barracloughi*, paratype. Spermatheca (Fig. 12) as in *promontorii*.
3. *Vermipardus* sp., *brevirostris* group, undescribed species from Kloof, KwaZulu-Natal. Spermatheca (Fig. 24) brownish, relatively small, ovoid, merging proximally with pale duct; external surface with minute, scattered, highly refractive, granule-like elevations.
4. *V. univittatus* (Stuckenberg), Cathedral Peak, KwaZulu-Natal. Spermatheca (Fig. 25) closely similar to 3. above, but less completely ovoid, proximal end shortened, surface similarly microgranulose.
5. *V. intermedius* (Stuckenberg), Grahamstown, Eastern Cape. Spermatheca (Fig. 26) brownish, microgranulose as in 3. and 4. above, differing in being hemispherical with deep hollow proximally in which duct is inserted.
6. *V. trisignatus* sp. n., paratype. Spermatheca (Fig. 23) brownish, microgranulose, almost hemispherical but a little more elongate than in *intermedius*, slightly concave proximally.

ANALYSIS OF RELATIONSHIPS

In the following analysis, characters that can be polarised with confidence are used to establish a cladistic framework for *Vermipardus*. This supplants my earlier attempt (Stuckenberg 1995). The italicised opening phrase of each numbered paragraph below specifies the apomorphic state. Thereafter, other character states which cannot yet be polarised are used to delineate lineages. The outcome is represented in the incomplete cladogram shown in Fig. 34.

1. *Aedeagal spiculae present*: the presence of these minute chitinous points (see Material and Methods above) is a specialisation; they are present in all species except *promontorii* and *barracloughi*.
2. *Setose protuberances present on incurved posterodorsal surfaces of synsternite*: only in *promontorii* (Stuckenberg 1995, Figs 6, 7) and *barracloughi* (Fig. 9).
3. *Spermatheca externally microgranulose*: see above; among the species investigated, only *promontorii* and *barracloughi* lack these microgranules; they are present in *univittatus, intermedius, trisignatus* and a representative of the *brevirostris* group, so are almost certainly present in those species of which the spermathecae have not yet been examined.
4. *Radial fork relatively short*: a feature of all species except *promontorii* and *barracloughi* which have a much deeper fork (Figs 57) with the ratio being not less than 0.75 and as much as 1.0 in some specimens (see Material and Methods above).

   Apomorphies 1–4 distinguish two monophyletic basal clades. They are ranked as subgenera which are designated provisionally as Subgenus 1 (for *promontorii* and *barracloughi*) and Subgenus 2 (all other lineages). The naming of these clades is deferred as extensive areas of South Africa still have to be searched for *Vermipardus* and may yield species that affect classification at the subgeneric level.
5. *Gonostyle strongly asymmetrical, developed in vertical plane*: the gonostyle

comprises a larger, more expanded dorsal section, and a narrower, offset, ventral, medially inclined branch (Stuckenberg 1960, Fig. 47; 1995, Figs 23, 29, 35); such an elaborate form is apomorphic and defines the *brevirostris* group (Stuckenberg 1995); in other species of Subgenus 2, the gonostyle is simpler, transversely extended, and more or less falcate or finger-shaped in dorsal view.

6. *Wing pattern reduced*: in Subgenus 2 the species have a definite, characteristic wing pattern, except *univittatus, sylphe* and *basuto* in which the wing is almost unpatterned (Stuckenberg 1995, Figs 41–43); this is interpreted as a derived condition. Such an interpretation is supported by variation seen in the intensity of wing patterning in *intermedius*; many specimens have the pattern typical of Subgenus 2, but others, especially females, have the wing almost plain and confusingly similar to the condition in the species of the *univittatus* subgroup.
7. *Mesonotum with a median and two lateral, shining black vittae, separated by narrow, anteriorly curved bands of pruinescence*: a feature of *brincki, trisignatus* and *whiteheadi* (Figs 15, 16, 31), but not of other species of Subgenus 2, therefore interpreted as apomorphic, and defining the *brincki* clade.
8. *Epandrium deeply concave posteriorly*: in *whiteheadi* and *trisignatus* the epandrium is unusually large (possibly also an apomorphy) and has a deep recess in the posterior margin (Figs 17, 28) differently shaped in these two species; such epandrial forms are unique; in *brincki* (Stuckenberg 1960, Fig. 53) the epandrium is unremarkable and has a broad, shallow apical concavity.
9. *Dorsal bridge with elongated arms*: in *whiteheadi* and *trisignatus* the dorsal bridge projects cephalad markedly (Figs 18, 29), an exceptional condition not found in *brincki* (Stuckenberg 1960, Fig. 49).
10. *Ventral aperture subovate with truncated proximal margin, apical guides bluntly rounded apically, short and only moderately extended posteriorly*: this condition distinguishes *sylphe* and *basuto*; it is interpreted as apomorphic because *univittatus* has a more common condition found also in *intermedius* and species of the *brincki* subgroup, in which the ventral aperture is narrowly lanceolate and the apical guides extend posteriorly as elongate, narrow, tapering projections close together and almost closing the distal end of the ventral aperture.

The outcome of this analysis is a rooted cladogram with two basal clades. Subgenus 1, presently with two widely separated species, appears to be geographically fragmented and relict. Subgenus 2 subdivides into two components, of which the *brevirostris* group is clearly monophyletic. The other component, provisionally called the *univittatus* group, cannot yet be confirmed as monophyletic through unequivocal apomorphies, but the group is defined by distinctive features as listed below. The *univittatus* group comprises an unresolved trichotomy of the *univittatus, intermedius* and *brincki* subgroups. The *univittatus* subgroup was previously found to be structured thus: *univittatus* + (*sylphe* + *basuto*) (Stuckenberg 1995); confirmation of apomorphy 10 should be sought when new material of the last two species becomes available. From apomorphies 8 and 9 above, the *brincki* group is confirmed as monophyletic and to be structured thus: *brincki* + (*whiteheadi* + *trisignatus*). In my previous study, *intermedius* was categorised as the sister-species of the three species here clustered in the *univittatus* subgroup, on the basis of characters of colouring and pattern of uncertain polarity. A restudy of *intermedius* shows that certain features of its hypopygium are not fully revealed in the dorsal view in which this species was previously illustrated (Stuckenberg 1960, Fig. 50). The gonostyles have a form unique to this species.

Subgenus 2 thus comprises an assortment of lineages which collectively and individually have a coherent distribution, ranging between KwaZulu-Natal and the South-West Cape. The only known overlap between the subgenera occurs on the Cape Peninsula. The two species of *Vermipardus* found there prove to be of entirely different cladistic ages; with regard to *promontorii*, this is another instance of the significance of the Cape Peninsula as a refuge for phylogenetically isolated invertebrates.

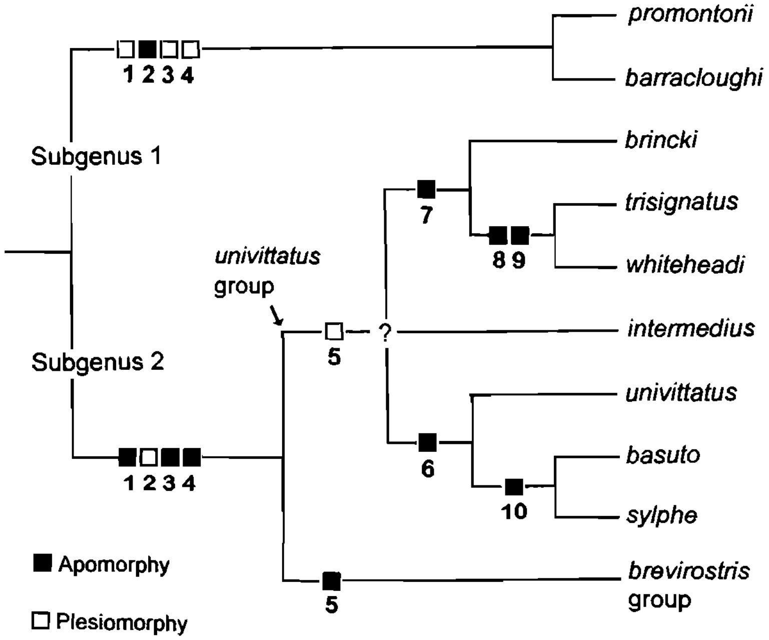


Fig. 34. Proposed cladogram for *Vermipardus*; the three subgroups of the *univittatus* group in Subgenus 2 constitute an unresolved trichotomy; for the *brevirostris* group, see Stuckenberg 1995, Fig. 48.

Characteristics of the clades

Subgenus 1: proboscis of variable length, ratio in ♂♂ 0.7–0.9, ♀♀ 0.6–1.0, usually shorter than fore femur; wing pattern weak, simple, costal cell not distinctly darkened, without a conspicuous dark area below stigma in cell r_1; radial fork deep, ratio 0.73–1.09 (both sexes); R_4 and R_5 only moderately divergent, R_{2+3} gently curved forwards apically; hind tibia and basitarsus conspicuously bicolorous (except *barracloughi*); aedeagal spiculae absent; setose protuberances postero-dorsally on synsternite, one on each inflexed margin proximal to socket of gonostyle; gonostyles broad in vertical plane, in dorsal view bluntly finger-like; spermathecae mushroom-shaped, gently convex distally, surface smooth, agranulose.

Subgenus 2: proboscis very variable in length but some species-groups characterised by short or long conditions (see below); wing pattern usually strong (eg. Figs 20, 21), costal cell obviously darker, a dark stigma present, dark areas below stigma in r_1 and apically in r_1, a conspicuous clear area between them, apex of first basal cell and borders of radial-sector dark, additional dark clouding in base of discal cell, in apex of wing and along most veins, often leaving clear areas within cells; radial fork shorter, ratio usually less than 0.70, R_4 and R_5 more divergent; R_{2+3} more strongly curved forwards apically, in some species angularly bent forwards, even with a short stump-vein at angle; aedeagal spiculae present; synsternite without setose protuberances; spermathecae small, brownish, subovoid to hemispherical, external surface microgranulose; gonostyles variably formed.

- *brevirostris* group: gonostyles as described above (character 5); proboscis always shorter than fore femur, ratio 0.5–0.8; hind tibia and basitarsus conspicuously bicolorous; wing strongly patterned as described for Subgenus 2; R_{2+3} strongly curved forwards apically or even angularly bent, sometimes a stump-vein at angle; epandrium with large apical recess surrounding proctiger; ventral aperture usually large, not narrow; aedeagus elongate to very elongate, with conspicuous spiculae; dorsal bridge elongate cephalad in correlation with aedeagal elongation; spermatheca ovoid (see descriptions of spermathecal forms above).
- *univittatus* group: gonostyles falcate in dorsal view; proboscis of variable length, ratio 1.0 or greater in most species, not known to be less than 0.8; Subgenus 2 type wing pattern well developed (except in *univittatus* subgroup); ventral aperture small, narrow, elongate; apical guides narrow, acuminate, and closely approximated, in most lineages; spermatheca subovoid to hemispherical with proximal concavity.
- *univittatus* subgroup: proboscis elongate, ratio 1.0–1.4; wing pattern weak, almost absent (character 6); R_{2+3} arched forwards apically; mesonotal pattern generally simplified (Stuckenberg 1995, Figs 11, 12); all legs similarly coloured and more or less unicolorous; epandrium with shallow, sometimes small apical recess; spermatheca in form of truncated ovoid (to be confirmed for *sylphe* and *basuto*); see character 10 above for relationships between the three species.
- *brincki* subgroup: proboscis moderately short to moderately long (ratio 0.8–1.2); mesonotum trivittate with dark pattern (character 7); humeri contrastingly pale; pleura mostly dark, a paler band across upper sternopleuron and hypopleuron; hind leg mostly shining dark brown, tibia and basitarsus with short, pale basal bands; Subgenus 2 wing pattern well developed, costal cell uniformly brownish; cell m_3 usually open, R_{2+3} strongly curved forwards apically; epandrium with extensive distal recess (shallow in *brincki*); spermatheca like a short cylinder with rounded end, concave below (to be confirmed for *brincki* and *whiteheadi*); ventral aperture small, narrow, elongate; apical guides acuminate, slender, approximated in dorsal view; aedeagus with numerous spiculae.
- *intermedius* subgroup: proboscis ratio 1.0–1.3; mesonotal pattern distinctive (Stuckenberg 1995, Fig. 10), median vitta narrowing strongly between

conspicuous delta marks; Subgenus 2 wing pattern developed but variable in intensity, normal in most specimens, weaker or almost absent in some (especially females – see character 6 above); R_{2+3} strongly curved forwards apically; hind leg with tibia and basitarsus dark brown except creamy whitish over short basal section; epandrium with broad, shallow distal concavity, a pale longitudinal strip of weak sclerotisation in midline; aedeagal spiculae lacking on shaft, present on upper surface and margin of broad lateral flanges at apex; gonostyle in dorsal view not curved, bluntly and obliquely terminated apically, base internally enlarged; ventral aperture small, elongate, narrow, apical guides acuminate, slender, close together; spermatheca hemispherical with deep proximal concavity; synsternite almost bare, contrastingly coloured orange-brown in comparison with preceding sternite 8 which is darker and abundantly setose. Monotypic at present.

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